

Natural History of the Peregrine Falcon in the Keewatin District of the Northwest Territories

GORDON S. COURT,¹ C. CORMACK GATES² and DAVID A. BOAG³

(Received 31 March 1987; accepted in revised form 28 September 1987)

ABSTRACT. A dense, productive population of peregrine falcons (*Falco peregrinus*) was studied for five years on a 450 km² study area located along the northwest coast of Hudson Bay. The mean internest distance of 3.3 km represents the highest nesting density on record for the species in the Arctic. Morphometric and plumage characteristics of adults in the population suggest they are intermediate between *F.p. tundrius* from farther north and *F.p. anatum* from boreal regions to the south and west. The migratory pathway used by this population of birds is similar to that used by peregrines from Alaska, northern Canada, and Greenland. Both timing of arrival on the breeding grounds and clutch initiation are influenced strongly by spring weather patterns. Nineteen species of birds and three species of mammals were used as prey; however, in most years the bulk of the diet consisted of six species of birds and one mammal. A dramatic increase in the density of territorial peregrines in a year of high microtine rodent abundance, coupled with changes in various measures of reproductive performance, suggested that use of lemmings by falcons can be significant in some years. Suggestions that peregrines lay fewer eggs in the arctic part of their range were not supported. Broods hatched asynchronously, with the last-hatched young dying in about one-half of all broods of four. Surviving last-hatched young in broods of four grew at rates similar to older nest mates. Brood size was as high as that for any tundra nesting peregrine population on record.

Key words: peregrine falcon, *Falco peregrinus tundrius*, morphology, migration, food, growth, productivity

RÉSUMÉ. On a étudié pendant cinq ans une population dense et productive de faucons pèlerins (*Falco peregrinus*) dans un territoire de 450 km² situé le long de la côte nord-ouest de la baie d'Hudson. La distance moyenne de 3,3 km entre les nids représente la plus haute densité de nidification relevée dans l'Arctique pour cette espèce. Les caractéristiques de la morphométrie et du plumage des adultes de cette population suggèrent qu'ils sont intermédiaires entre le *F.p. tundrius* des régions plus au nord et le *F.p. anatum* des régions boréales au sud et à l'ouest. Le parcours de la migration de cette population d'oiseaux est semblable à celui des faucons pèlerins de l'Alaska, du nord du Canada, et du Groenland. Le moment de l'arrivée sur les lieux de reproduction et celui du début de la ponte sont tous deux fortement influencés par les particularités du climat printanier. Dix-neuf espèces d'oiseaux et trois espèces de mammifères leur servaient de proies; au cours de la plupart des années cependant, la plus grande partie de leur alimentation provenait de six espèces d'oiseaux et d'un seul mammifère. Au cours d'une année où les rongeurs microtinés étaient très abondants, la nette augmentation de la densité des faucons pèlerins qui avaient établi leur territoire, ainsi que des changements dans diverses mesures de leur performance reproductive, ont suggéré que certaines années les faucons peuvent consommer un grand nombre de lemmings. On n'a rien trouvé pour confirmer l'hypothèse que les faucons pèlerins pondent moins d'oeufs dans la partie arctique de leur habitat. Les couvées éclosaient de façon asynchrone, et le dernier éclos mourait dans environ la moitié des couvées de quatre oisillons. Les derniers éclos qui survivaient dans les couvées de quatre oisillons grandissaient au même rythme que les oisillons éclos avant eux. Les couvées étaient aussi importantes que celles de n'importe quelle population de faucons pèlerins relevée jusqu'à maintenant et nidifiant dans la toundra.

Mots clés: faucon pèlerin, *Falco peregrinus tundrius*, morphologie, migration, alimentation, croissance, productivité

Traduit pour le journal par Nésida Loyer.

Реферат: Плотная, продуктивная популяция перелётных соколов (*Falco peregrinus*) изучалась в течение пяти лет на наблюдаемой площади размером в 450 км², находящейся вдоль северо-западного побережья Гудзонова залива. Среднее расстояние между гнёздами (3,3 км) представляет собой самую высокую известную плотность гнездования этого вида в Арктике. По своему размеру и оперению взрослые птицы этой популяции являются чем-то средним между (*F.p. tundrius*), из более северных районов, и (*F.p. anatum*), из boreальных более южных и западных районов. Миграционный путь этой популяции птиц похож на миграционный путь перелётных соколов из Аляски, Северной Канады и Гренландии. И время прилета на место размножения и начало яйцекладки сильно зависят от весенней погоды. Соколы охотились на девятнадцать видов птиц и три вида млекопитающих, однако, по данным наибольшего количества лет, основная часть питания состояла из шести видов птиц и одного вида млекопитающих. Очень существенное увеличение плотности популяции гнездящихся соколов в год обилия леммингов, а также изменения в разных

¹Department of Zoology, University of Otago, Dunedin, New Zealand; formerly Department of Zoology, University of Alberta, Edmonton, Alberta, Canada T6G 2E9

²Renewable Resources, Government of the Northwest Territories, Fort Smith, Northwest Territories, Canada X0E 0P0

³Department of Zoology, University of Alberta, Edmonton, Alberta, Canada T6G 2E9

©The Arctic Institute of North America

показателях репродуктивной деятельности этих птиц, говорят от том, что в некоторые годы употребление леммингов соколами бывает значительным. Данных, указывающих на то, что перелётные соколы несут меньше яиц в арктическом районе своего ареала, найдено не было. Выводки вылуплялись неодновременно, причем птенцы, вылупившиеся последними, умирали в примерно половине из всех выводков, состоящих из четырех особей. Темп роста птенцов, вылупившихся последними, но выживших в выводках, состоящих из четырех особей, не отличался от темпа роста их старших братьев и сестер. Размер выводков был не ниже, чем в любой другой известной популяции перелётных соколов, гнездящихся в тундре.

Важные слова: перелётный сокол, *Falco peregrinus tundrius*, морфология, миграция, пища, рост, продуктивность.

INTRODUCTION

The peregrine falcon (*Falco peregrinus* Tunstall) is probably the most studied of all raptorial birds, and a large portion of all studies of this species were of populations nesting at arctic latitudes. Studies in the Nearctic have consisted of surveys of population size and nesting success (Calef and Heard, 1979; Kuyt, 1980; Burnham and Mattox, 1984; Falk and Møller, in press), including large-scale surveys concerned with assessing the impact of pesticide pollution on breeding populations (Cade and Fyfe, 1970; Fyfe *et al.*, 1976). More detailed studies of the breeding biology and ecology of arctic populations are less common and, with the exception of Cade (1960), have concentrated mainly on the late incubation and nestling phases of the nesting cycle (Enderson *et al.*, 1972; Burnham, 1975; Harris and Clement, 1975; Burnham and Mattox, 1984; Falk *et al.*, 1986). Fyfe (1969) identified large areas of potential nesting habitat for this falcon in arctic Canada. To date, much of this area remains to be surveyed. However, recent work has identified several dense and productive populations (Alliston and Patterson, 1978; Calef and Heard, 1979; Bromley, in press). For the most part, these studies have been concerned with documenting the size and productivity of previously unknown populations. Little work has been done to document the basic ecology of the species in the Northwest Territories.

From 1981 to 1985 we studied a population of peregrines nesting on coastal Hudson Bay, near the community of Rankin Inlet, N.W.T. The population was largely unknown until 1980, when preliminary work indicated a very dense and productive population that, particularly in terms of prey use, was unlike most arctic peregrine populations yet studied. The small size of the study area and high density of this population enabled us to conduct research on aspects of peregrine falcon biology that are poorly known, rather than concentrating on another survey of population size and reproductive success. We examined the morphology of breeding adults, recorded the distribution and density of nesting pairs, their arrival on the breeding ground, nesting behaviour, nestling growth and brood reduction, and the nature of their migration through band returns. Additionally, we

were able to monitor productivity of this species within a circumscribed patch of nesting habitat for five consecutive breeding seasons. This allowed an accurate assessment of the breeding performance of an arctic peregrine population and served to show up potential biases of short-term surveys or field work performed late in the breeding season.

STUDY AREA

The study area is located near the community of Rankin Inlet, N.W.T., on the western coast of Hudson Bay (62°49'N, 92°05'W) (Fig. 1). Summers in this region are typically short and cool, with July mean high and low temperatures of 13.1° and 4.5°C respectively. Spring thaw begins in mid-May, reaching a peak by the first week of June. Ice cover on small lakes and ponds begins to melt at this time; however, landfast sea ice persists until the second week of July (Fig. 2). Annual precipitation figures average 118.0 cm of snow and 16.0 cm of rain.

The study area encompassed approximately 450 km². The landscape is typical of tundra regions of Canada, with low rolling hills interspersed with numerous ponds and lakes. Geologically the area is dominated by altered intermediate volcanic rock and derived amphibole schist and gneiss (Wright, 1967). Rock outcrops up to 53 m in height are a prominent feature of the landscape and are particularly well developed as islands in Rankin Inlet. Outcrops with rock faces large enough to be of significance to cliff-nesting raptors occur as much as 6 km inland and on islands up to 4 km out to sea.

Ridge tops, upland areas, and well-drained slopes are covered with a formation of lichens, moss, and low shrubs. Labrador tea (*Ledum palustre*), mountain cranberry (*Vaccinium vitis-idaea*), and crowberry (*Empetrum nigrum*) are the dominant vascular plants. Bell heather (*Cassiope tetragona*) occurs in moist low-lying areas and rock crevices. Vegetation on most slopes and hillsides consists of combinations of heaths with *Dryas integrifolia*, *Carex* spp., *Cassiope*, and lichens (Maher, 1980). Fifty-three species of birds and ten species of mammals were recorded on the study area (Court, 1986).

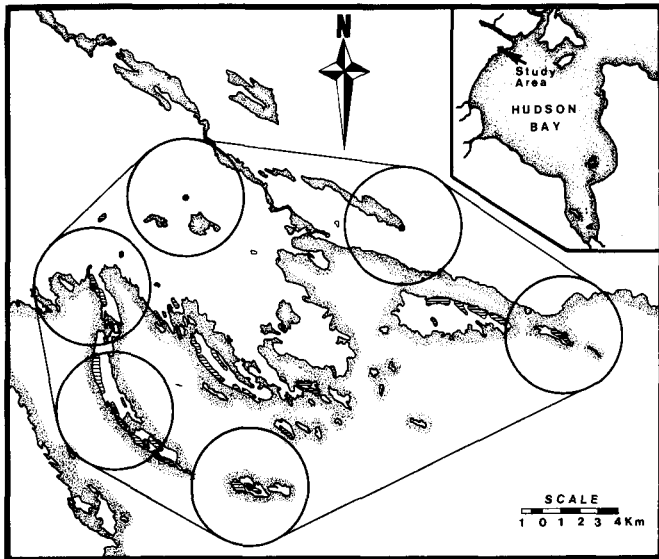


FIG. 1. Map of the Rankin Inlet study area showing boundaries defined by the method of Ratcliffe (1980).

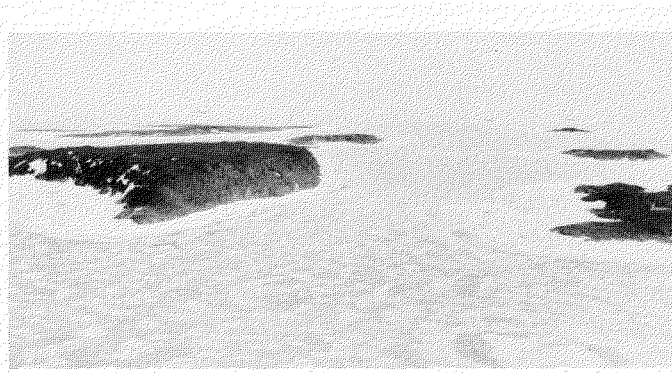


FIG. 2. The Rankin Inlet study area in late June. Landfast sea ice remains in the area until late July. (Photo by G. Court.)

METHODS

Peregrine falcons in the Rankin Inlet area were studied first in 1980 by the Department of Renewable Resources, Government of the N.W.T. Detailed information on nest site distribution, occupancy, and productivity was collected by the authors between 1981 and 1985. Field seasons were from May to September each year.

Beginning in mid-May the study area was surveyed by snowmobile for arriving falcons. Arrival times of all primary prey species were noted and relative abundance of each species was monitored throughout the nesting season. Most prey species taken by peregrines were small (less than 100 g) and were usually consumed in their entirety. Plucked feathers were usually blown away from all but the most sheltered nest ledges, making prey use impossible to assess quantitatively. However, the timing of prey use and the percentage of pairs using a species were determined by noting prey remains at nests and at plucking points on each cliff.

The chronology of events during the early nesting period of all pairs was monitored after the first week of June. Dates of

clutch initiation were recorded from 1982 to 1984. First egg dates were obtained by backdating from known laying dates, assuming a 48-hour interval (Nethersole-Thompson, 1931) between eggs. In all years but 1981 complete surveys of all known and potential nest sites were undertaken in mid-June (early incubation) and again in early July (late incubation) using a helicopter. Data on total egg production, nest failures, or egg losses were obtained during these surveys. Brood size was calculated using the number of young present at the nest when nestlings were three weeks of age.

The growth rate of young in asynchronously hatched broods of four was measured in 1983 and 1984. In these years nests were routinely visited during the time of hatch, hatch order was determined, and each chick was individually marked. Age was determined by observing hatch progress and, in some cases, predicting time of hatch; chicks still moist from the egg were assumed to be less than 24 hours old. In most cases time of hatch was obvious, but occasionally age had to be estimated from parameters such as the day on which eggs pipped (assuming hatch 2 days following pipping [H. Armbruster, pers. comm. 1983]) or from body weight comparisons with chicks from the same hatch position and of known age. The margin of error in estimates is believed to have been no greater than 1 day. The body weights of chicks were recorded on each nest visit until the chicks were 30 days of age. Growth curves were compared graphically, and an analysis of covariance was used to compare the slopes of weight gain over time for chicks from all four hatch positions. Only data from the straight-line portion of growth curves were used. Because they are dimorphic, male and female nestlings were analyzed separately.

At four weeks of age young falcons were banded with a standard U.S. Fish and Wildlife lock-on band on the right leg. A custom-manufactured blue anodized band was fitted to the opposite tarsus. The colour bands were individually marked with a three-digit alpha-numeric code and could be read from as far as 40 m using a 45 power spotting scope. Adult falcons were trapped as they arrived on the breeding area and at the nest when eyasses were small. Capture techniques are not described in detail so as to limit possible abuses. Adults were sampled for blood and banded in the same manner as the nestlings. To allow comparisons with *F.p. tundrius* (White, 1968), adults were weighed and measurements of their wing chord and tail length taken (Godfrey, 1986). Wing and tail lengths of adults from the study population were compared statistically to those of a captive sample of *F.p. anatum* originating from boreal regions of Canada (measurements taken at Canadian Wildlife Service, Wainwright, Alberta).

Terms used to describe nesting activity were based on Postupulsky (1974) and are summarized as follows:

- Territory — an area that contained one or more nest sites within the range of a known or inferred pair of actual or potential breeders.
- Nest site — the actual site of the nest. More than one nest site may have been present within the territory of a pair of birds but used in different years.
- Occupied territory or occupied nest site — a territory or nest site where one pair of birds was present at some time during the breeding season, although eggs may not have been present, and where the presence of birds was made obvious by defence behaviour exhibited toward conspecifics and potential predators, including humans.
- Production — the total number of young fledged or raised to

an advanced stage of development (35 days old) from all productive territories.

- Productivity — expressed as the mean number of young fledged per occupied territory.

Density of nesting pairs and the actual size of the study area were calculated according to Ratcliffe (1980). This entailed calculating the average minimum distance between each nest site of occupied territories (mean interest distance). Mean interest distance was used to compute hypothetical boundaries for the study area, which in turn allowed calculation of study area size (Ratcliffe, 1980). Although originally suggested as a means of measuring density in inland areas where nesting habitat is relatively homogeneous, this method serves adequately to establish study area size for the Rankin Inlet population. Nineteen territories, the median number of territories occupied between 1981 and 1985, were used in making these calculations.

RESULTS

Morphology of Adults

White (1968) based his description of *F.p. tundrius* on the fact that tundra birds were smaller in body size than other peregrines in North America and on plumage characteristics he believed typical of *F.p. tundrius*. In brief, adult *tundrius* were distinguished from *F.p. anatum* and *F.p. pealei* in that the overall plumage was "lighter," particularly in the head and ventral areas. Accordingly, typical *F.p. tundrius* specimens have a large white auricular area (ear patch) on the head with the malar bar (sideburn) below the eye, columnar in shape. The breast is generally less extensively marked than in other subspecies and the wash or ground colour of the ventral plumage was noted as faint to lacking (White, 1968).

White (1968) did not provide error terms with the measurements of his sample population of *F.p. tundrius*, thus precluding statistical comparisons of his data with the birds from Rankin Inlet. Birds from these two samples are very similar in body weight and tail length, but the mean wing length for the Rankin Inlet birds was longer than that obtained by White (1968) and closer to that for the sample of *F.p. anatum*. Statistical comparison of the study population with the sample of *F.p. anatum* showed that, with the exception of wing length of males, the Rankin Inlet birds are significantly smaller in body size (Table 1).

Of 47 adult peregrines captured at Rankin Inlet, 38 showed plumages similar to that described by White (1968). As he predicted, males more often than females represented the "typical" tundra peregrine in plumage. Head and face characteristics of the Rankin Inlet birds varied from exceptionally light, with a superciliary stripe (eyebrow) and large, white auricular areas as described by White, to atypically dark birds with no auricular space at all and the malar stripe developed as a black cap over the entire head (Fig. 3). There was also considerable variation in breast markings, particularly in the females. Some individuals showed very heavy barring on the breast and, similar to *F.p. anatum*, the wash of the paler parts of the ventral plumage was often rufous.

Density and Nest Site Characteristics

The number of occupied territories on the study area varied from 17 in 1981 to 26 in 1985. The smaller number is probably the least accurate, as observers were new to the study area in that year. It is unlikely that any territorial pairs were overlooked on the study area from 1982 to 1985. The 26 pairs in 1985 was exceptional; the usual density was 19–20 occupied territories. A mean interest distance (\pm SD) of 3.3 ± 2.0 km was calculated for the study area. Actual nearest neighbour distances ranged from 700 to 9850 m. The study area size was 450 km² (Fig. 1). Thus a maximum density of occupied nest sites per unit area (1985) was approximately one pair of peregrines for every 17 km² (26/450). It should be noted that this density is conservative, because approximately 235 km² of the study area consisted of ocean surface.

The nesting activities of peregrines over the five years involved the use of 29 separate cliffs. Of these, 21 bordered on the ocean or were within 150 m of the shoreline. Three other cliffs were located in the centre of islands or peninsulas, and 5 were located inland on the mainland; all were within 300 m of substantial water bodies. The cliff faces used for nesting varied between 7 and 30 m in height. The lowest nest was 4 m from the base of a 12 m face and the highest was 26 m from the base of a 30 m face. The use of alternative nest sites was documented through colour banding of adults. The distance between cliffs used by the same pair in different years ranged from 550 to 2025 m, with a median of 950 m ($n = 8$). Although pairs occasionally changed cliffs, fidelity to territories was high, with movement of banded adults

TABLE 1. Morphometric comparison of peregrine falcons from the Rankin Inlet population, the original sample used by White (1968) to define *Falco peregrinus tundrius*, and a sample population of *Falco peregrinus anatum*

Subspecies	Sample	Males			Females		
		Wing chord (mm)	Tail length (mm)	Weight (g)	Wing chord (mm)	Tail length (mm)	Weight (g)
<i>F.p. tundrius</i>	White (1968)	n =	64	64	12	62	19
		\bar{x} =	308.3	140.5	610.9	351.8	167.8
<i>F.p. tundrius</i>	Rankin Inlet	n =	14	15	15	32	31
		\bar{x} =	318.0 ± 7.65^1	139.4 ± 5.01^2	607.0 ± 42.42	361.3 ± 6.28^3	164.4 ± 5.79^4
<i>F.p. anatum</i>	C.W.S. Wainwright	n =	14	14	14	16	16
		\bar{x} =	320.7 ± 8.70^1	147.7 ± 3.07^2	600.0 ± 37.62	365.8 ± 8.15^3	175.6 ± 3.52^4

Statistical comparison between Rankin Inlet sample and C.W.S. Wainwright sample:

¹Student t-test df = 27 t = 0.88 P = 0.39.

²Student t-test df = 27 t = 5.33 P < 0.01.

³Student t-test df = 46 t = 2.13 P = 0.02.

⁴Student t-test df = 46 t = 7.08 P < 0.01.

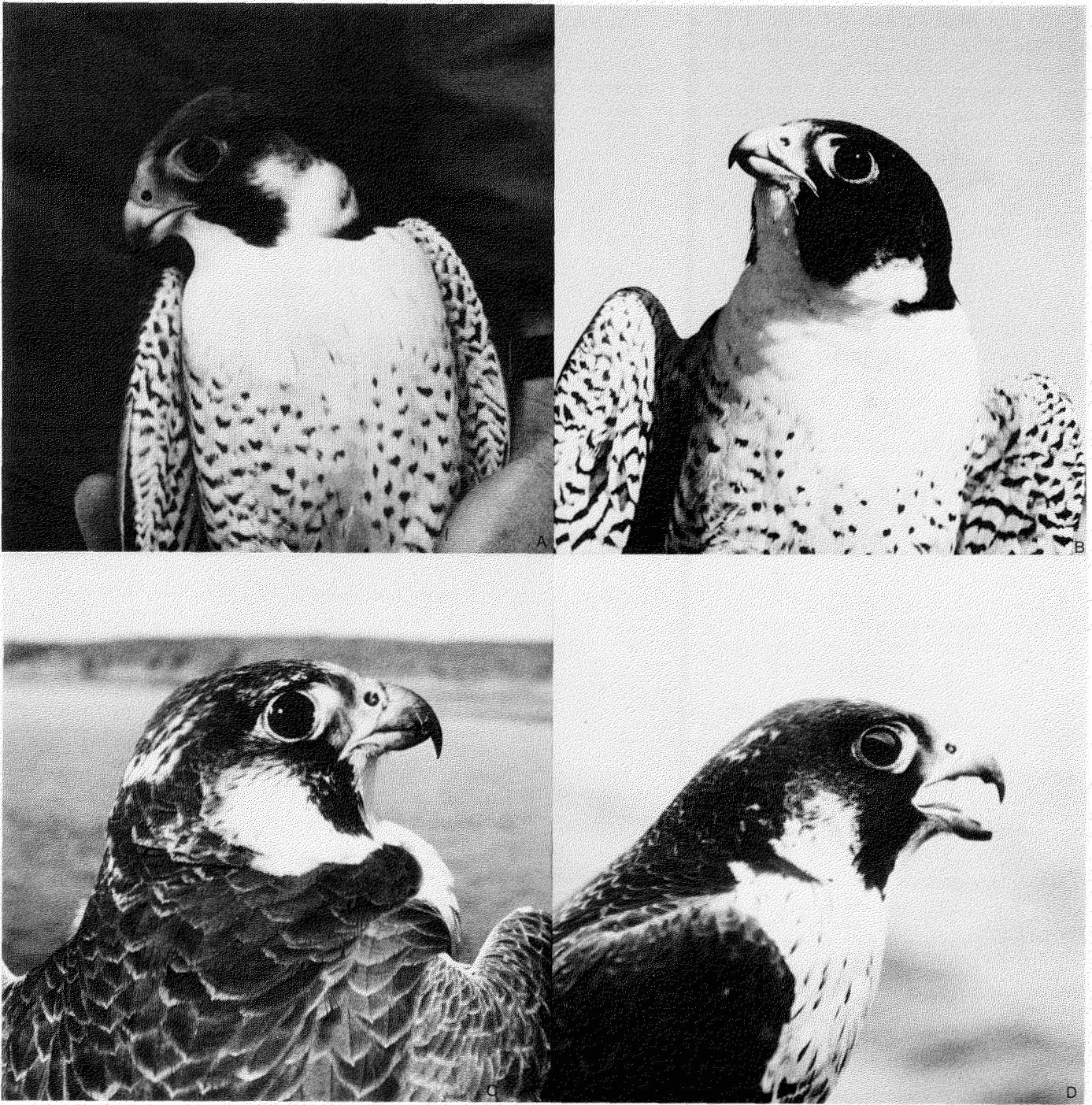


FIG. 3. Variation in head plumage of adult peregrine falcons from Rankin Inlet. A) Male with large white auricular area and malar stripe columnar in shape. (Photo by S. Devine.) B) Male with no malar stripe. (Photo by G. Court.) C) Light-coloured female with superciliary stripe and light feathers on nape. (Photo by M. Bradley.) D) Darker female typical of birds breeding at Rankin Inlet. (Photo by M. Bradley.) Individuals shown here represent variation, not extremes, in plumage characteristics; darker and lighter plumages of both sexes were encountered in the population.

($n=47$) between territories in different years recorded only once in the five years of the study (Court, 1986).

Nest sites on cliffs were abundant; of 68 breeding attempts recorded between 1981 and 1984, precisely the same nest was reused on only three occasions, never in successive years. Peregrine falcons lay their eggs in a shallow depression or scrape, which is scratched into the substratum of the nest ledge (Burnham, 1975; Cade, 1982). Three different types of sub-

strata underlay the scrapes made by falcons in the Rankin Inlet population. Loose soil, often including small rock chips and pieces of dead vegetation, made up the substratum of 17(27%) scrapes, ledges of thick turf supported 18(29%) nests, and abandoned rough-legged hawk nests made up the remaining 27(44%) substrata. Most nests were poorly sheltered from above, with only three located on ledges under overhanging rock. Protection from mammalian predators was also poor; all

but 7 of 68 clutches produced between 1981 and 1984 were accessible to humans without full climbing gear.

Most nest sites used by peregrines had a southern component to their exposure: 20 faced south or southwest, 5 northeast, 3 north, and 1 west. Pairs nesting on north-facing sites showed no significant difference in the mean number of young fledged (including sites that failed) compared to those nesting on cliffs with a southern exposure (north-facing: $n = 23$ $\bar{x} = 2.26 \pm 1.48$ young, versus south-facing: $n = 58$ $\bar{x} = 2.34 \pm 1.15$; Mann-Whitney U-test $U = 632.0$ $P = 0.70$).

Arrival on the Breeding Grounds

Peregrine falcons were seen on the study area as early as 10 May. However, pairs of birds were rarely recorded at nest sites earlier than 20 May. Of six cliffs routinely checked each spring from 1982 to 1984, pairs were recorded at nest sites before 20 May on only three occasions, but by 28 May of each year all six nest sites had pairs regularly in attendance.

The arrival of peregrines on the study area appeared to be influenced by spring weather. An unusually heavy snowfall was recorded in this area in the spring of 1983. Blizzard conditions during the second half of May contributed to snowfall records nearly triple those for the same period in 1982 and over 50 times

TABLE 2. Mean temperature and total precipitation for late May and early June in Rankin Inlet, N.W.T., 1982-84

Year	16-31 May		1-15 June	
	Mean temperature (°C)	Total precipitation (mm)	Mean temperature (°C)	Total precipitation (mm)
1982	-3.2	7.3	-1.1	5.4
1983	-6.6	20.2	0.9	96.8
1984	-2.5	0.4	2.5	5.2
Mean (1981-85)	-3.4	10.24	1.21	22.78

those for 1984 (Ministry of Transport Records, Rankin Inlet) (Table 2). In 1983 peregrines were seen as early as 10 May, but they disappeared with the onset of poor weather on 16 May and were not seen again until 25 May. Of six sites monitored for returning peregrines in 1982, all had pairs in attendance by 25 May, and in 1984 five of six were attended by pairs on the same date. On this date in 1983, however, only two of six sites had pairs in attendance.

Both sexes of peregrine arrived on the breeding grounds simultaneously. The male:female ratio of the first 10 birds to be seen in each of the years 1982-84 was 6:4 in 1982, 4:6 in 1983, and 5:5 in 1984. There was no evidence to suggest that previously mated pairs arrived at the same time. Colour marking showed that individuals that had bred successfully at a cliff the previous season may return some days before their mate of the previous year. In one case, a marked male was present at a nest cliff for eight days before the marked female from the previous season arrived. She was successful in driving away another unmarked female that had occupied the cliff in the interim.

Peregrines at Rankin Inlet perched at cliffs upon arrival but did not show a strong attachment to these sites until the last week of May. Before this date it was difficult to guarantee their presence at any nest cliff when using conventional survey techniques. Birds that had recently returned to the breeding grounds would frequently fly silently from the nest cliff and leave the area if approached by an observer. Defence of the nest site against humans through protest vocalizations was rarely recorded until late in the last week of May or the first week of June. Conversely, aggression between peregrines perched at the same cliff often began immediately upon arrival. Fighting over nest sites was intense throughout May, particularly between adult males, but was rarely recorded after clutch initiation.

Prey Use

Nineteen species of birds and three species of mammals were recorded as prey items at Rankin Inlet (Table 3). The majority of

TABLE 3. Prey species used by peregrine falcons nesting at Rankin Inlet, 1981-85

Birds		Status	Abundance	Mean date of arrival	Frequency
Northern Pintail	<i>Anas acuta</i>	BL	C	2 June	3
Oldsquaw	<i>Clangula hyemalis</i>	BL	C	6 June	3
Common Eider (juveniles)	<i>Somateria mollissima</i>	BL	C	30 July	2
Rock Ptarmigan	<i>Lagopus mutus</i>	BL	R	Before 10 May	4
Semipalmated Plover	<i>Charadrius semipalmatus</i>	BL	C	3 June	3
Lesser Golden Plover	<i>Pluvialis dominica</i>	BL	UC	2 June	2
White-rumped Sandpiper	<i>Calidris fuscicollis</i>	M	C	10 June	2
Baird's Sandpiper	<i>Calidris bairdii</i>	M	C	1 June	2
Dunlin	<i>Calidris alpina</i>	BL	UC	10 June	2
Semipalmated Sandpiper	<i>Calidris pusilla</i>	BL	C	8 June	3
Red Phalarope	<i>Phalaropus fulicaria</i>	BL	R	8 June	1
Arctic Tern	<i>Sterna paradisaea</i>	BL	UC	Unknown	1
Long-tailed Jaeger	<i>Stercorarius longicaudus</i>	BL	R	12 June	1
Black Guillemot	<i>Cephus grylle</i>	BL	C	19 June	2
Horned Lark	<i>Eremophila alpestris</i>	BL	C	21 May	4
Water Pipit	<i>Anthus spinoletta</i>	BL	C	25 May	4
Palm Warbler	<i>Dendroica palmarum</i>	A	—	—	*
Lapland Longspur	<i>Calcarius lapponicus</i>	BL	C	26 May	4
Snow Bunting	<i>Plectrophenax nivalis</i>	BL	C	Before 10 May	4
Mammals					
Arctic Ground Squirrel (juveniles)	<i>Spermophilus parryii</i>	BL	C	—	2
Collared Lemming	<i>Dicrostonyx groenlandicus</i>	BL	V	—	2
Brown Lemming	<i>Lemmus sibiricus</i>	BL	V	—	2

Status: BL = breeds locally; M = migrant; A = accidental.

Abundance: C = common; UC = uncommon; R = rare; V = highly variable.

Frequency codes: 1 = recorded at up to 25% of nests; 2 = recorded at 25-50% of nests; 3 = recorded at 50-75% of nests; 4 = recorded at 75-100% of nests; * = recorded on only one occasion.

the avian prey species taken arrived on the study area after peregrines and were usually used immediately upon arrival. Species migrating through the area were used when available, while those breeding locally were used (as adults and juveniles) throughout the breeding season.

Only rock ptarmigan (*Lagopus mutus*) and snow buntings (*Plectrophenax nivalis*) were present on the study area when peregrines arrived each spring. Both were important as prey at this time, based on their remains at all nest cliffs. Ptarmigan were rarely seen on the study area after the first week of June and either left the area or dispersed onto the tundra at very low densities. No evidence of breeding was recorded for ptarmigan in the area, and remains of these birds were never recorded at cliffs after early June. Snow buntings breed locally and were recorded as prey items throughout the breeding season.

In addition to the snow bunting, three other species of passerine birds, horned lark (*Eremophila alpestris*), Lapland longspur (*Calcarius lapponicus*), and water pipit (*Anthus spinoletta*) were important prey species for the study population. All three arrived before waterfowl or shorebirds and were used extensively early in the season. Adults of all four passerine species were used throughout the season and, at some falcon nests, fledglings of these species provided the bulk of the food used to raise young peregrines.

Waterfowl remains were rarely found at nest cliffs before the first week in August. It was about this time that female peregrines began taking a more active role in hunting, and their larger size was reflected by the presence of large prey species in the nest. Both adult and juvenile pintails (*Anas acuta*) and oldsquaw (*Clangula hyemalis*) were recorded as prey items, but only juvenile common eiders (*Somateria mollissima*) were taken.

Black guillemots (*Cepphus grylle*) congregated at sea ice cracks and open leads in the study area as early as 19 June. They began to occupy colonies during the first week of July, shortly before breakup. Most colonies were situated at the bases of sea cliffs, where the birds nested among the rock rubble. Peregrines nesting above or near these colonies preyed upon guillemots to a large extent. Three pairs of peregrines in the study area annually specialized on adult guillemots while raising their young, although passerines supplemented these diets. There was no evidence of predation on juvenile guillemots.

Arctic ground squirrels (*Spermophilus parryii*) and two species of lemming, *Dicrostonyx groenlandicus* and *Lemmus sibiricus*, were recorded as prey items. Arctic ground squirrels

(juveniles) were recorded at eight nest sites within the study area, and evidence of use of this species was obtained in all years of the study. Populations of four microtine species (*Dicrostonyx groenlandicus*, *Lemmus sibiricus*, *Microtus pennsylvanicus*, and *Clethrionomys gapperi*) peaked in the southern Keewatin in 1985 (F. Mallory, pers. comm. 1985). The peregrines nesting at Rankin Inlet used lemmings as prey in 1985, with remains, often several whole carcasses, recorded at about one-half the nests in the study area. The number of pairs using lemmings was probably underestimated because of a lack of identifiable remains at nest sites. Although peregrines attempted to pluck lemming carcasses, little remained of these mammals after feedings.

Like the sympatric population of rough-legged hawks (*Buteo lagopus*), the peregrine population apparently responded numerically to the peak in microtine numbers in 1985 (Court, 1986; Court *et al.*, in press). The population increased by six territorial pairs (30%), the percentage of pairs producing a clutch increased, the mean brood size for the population was greater in this year than in any other year of the study, and the total number of young produced on the study area was nearly double that in any of the previous four years (Table 4).

The Incubation and Nestling Period

The earliest record of clutch initiation for the Rankin Inlet population was 1 June; the latest was 19 June. Dates of clutch completion (four eggs) for these records would be 6 or 7 June for the early case and 24 or 25 June for the late case. Most pairs (91%) initiated a clutch before 15 June. The mean date of clutch initiation for three consecutive seasons was 7 June (1982), 13 June (1983), and 8 June (1984), making the mean date of clutch initiation significantly different among years (Kruskal-Wallis Test $H = 14.84$ $P < 0.01$) (Fig. 4). Multiple comparison tests (Conover, 1980) showed that dates of clutch initiation in 1983 were significantly later than in either 1982 or 1984. Thus, as with the arrival times, there was a significant delay to the start of breeding in 1983. Precipitation figures for May and June of that year were much higher and temperatures lower than for the same period in 1982 and 1984 (Table 2).

A clutch of four eggs was the most common, found in 67% of all nests (Table 5). Clutches of two to four eggs hatched successfully; however, the single clutch of one egg was abandoned during the first week of incubation. Mean clutch size (\pm SD) was 3.62 ± 0.59 ($n = 84$). Clutch size did not vary signifi-

TABLE 4. Breeding success of peregrine falcons nesting at Rankin Inlet, N.W.T., 1981-85

	1981	1982	1983	1984	1985	1981-85 (mean)
Occupied territories	17	19	19	20	26	20.2
Pairs laying (%)	16(94)	17(89)	17(89)	16(80)	25(96)	18.2(90)
Eggs produced	unknown	63	60	58	92	—
Pairs producing young (%)	15(88)	14(74)	14(74)	14(70)	20(77)	15.4(76)
Pairs fledging young (%)	15(88)	14(74)	13(68)	12(60)	20(77)	14.8(73)
Young hatched	unknown	39	42	43	unknown	—
Production	36	35	36	37	61	41
Productivity	2.12 ± 1.11	1.84 ± 1.30	1.89 ± 1.45	1.85 ± 1.66	2.35 ± 1.47	2.03 ± 1.41^1

¹1-way ANOVA $F = 0.54$ $df = 4,96$ $P = 0.70$.

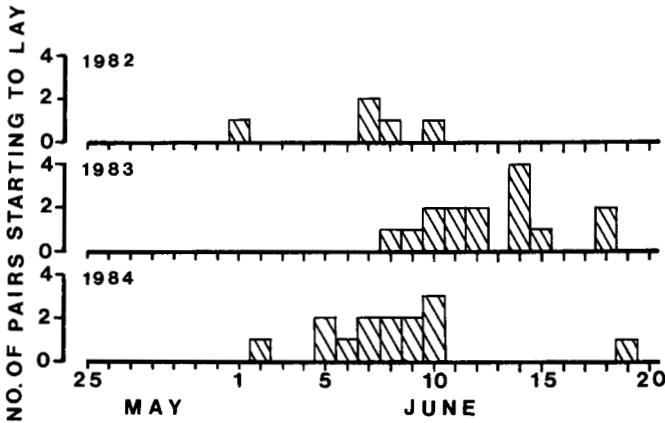


FIG. 4. Dates of clutch initiation for peregrine falcons nesting at Rankin Inlet for 1982, 1983, and 1984.

TABLE 5. Number of clutches of different sizes for peregrine falcons nesting at Rankin Inlet, N.W.T., 1981-85

Year	Number of clutches of following sizes				Total	Mean \pm S.D.
	1	2	3	4		
1981	0	1	3	5	9	3.44 \pm 0.73
1982	1	0	2	14	17	3.71 \pm 0.77
1983	0	0	8	9	17	3.53 \pm 0.51
1984	0	1	4	11	16	3.63 \pm 0.62
1985	0	0	8	17	25	3.68 \pm 0.47
All years	1	2	25	56	84	3.62 \pm 0.59 ¹

¹Kruskal Wallis 1-way ANOVA $H = 3.33$ $P = 0.50$.

cantly from year to year (Table 5). We found no significant difference between the mean clutch size of the Rankin Inlet population ($n = 84$) and that reported by Hickey (1942) for a pre-pesticide population in the eastern United States ($n = 282$) (Mann Whitney U Test $U = 11185.5$ $P = 0.36$).

Hatching dates for the first egg in a clutch ranged from 2 July to 21 July (mean 9 July). Clutches hatched asynchronously. Asynchrony was particularly obvious in larger broods; however, even some broods of two showed a noticeable difference in the size of chicks. Although the timing of hatch was difficult to ascertain accurately for all broods, the pattern of hatch observed most frequently included: relative synchrony in the hatch of the first and second eggs, the third egg hatching 1 to 1.5 days later, and the fourth egg 2 days after the third. These patterns suggest that most females in the study population began effective incubation either shortly before or after laying the second egg. Nevertheless, considerable variation in the degree of asynchrony was observed as oldest and youngest members of broods were occasionally separated by as little as 3 days and in other cases by as much as 5 days.

Asynchronous hatching resulted in a wide range in size of the members of a brood; freshly hatched chicks weighed as little as 36 g, while 5-day-old siblings weighed 100-140 g (Fig. 5). These differences apparently introduced a competitive disadvantage to youngest members of some broods, as these died in 45% (5/11) of broods of four chicks produced in 1983 and 1984. All mortality occurred before the chicks were 5 days old.

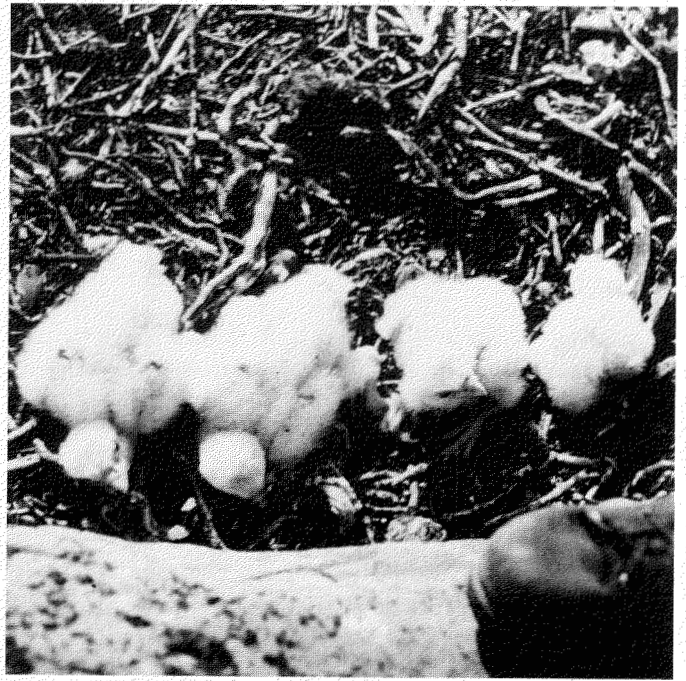


FIG. 5. An asynchronously hatched brood of four nestling peregrine falcons from Rankin Inlet. The age of the youngest nestling is 1 day, the oldest, 6 days. (Photo by G. Court.)

Mortality associated with asynchronous hatching accounted for a 7% (6/85) reduction in the total number of chicks hatched in these years. Starvation was the probable cause of mortality, as a single chick that was recovered was grossly underweight (55 g at 5 days) compared to nestlings of the same age but from different hatch positions. At one nest the adult female was seen to remove a dead chick from the nest, but she later returned with the carcass and fed it to the remaining chicks. The lack of remains at other nests suggests that other dead chicks may have been treated in a similar manner.

A plot of weight gain through time for asynchronously hatched broods of four ($n = 6$) showed that last-hatched nestlings that survived the first few days of life did not suffer a disadvantage through lack of access to food, since weight gain during their first 30 days was similar to that of other siblings (Figs. 6, 7). There was no significant difference in the slope of the straight-line portions of growth curves for chicks from all four hatch positions (Analysis of Covariance: Males — Equality of slopes $F = 1.41$ $P = 0.25$; Females — Equality of slopes $F = 0.19$ $P = 0.89$). It is possible that the last-hatched young, although they survived and grew normally, may have been slightly delayed in their weight gain very early in life (less than 5 days old); however, the data were insufficient to test for such differences.

Broods of three young were the most common, found in 47% of all nests (Table 6). Mean brood size (\pm SD) was 2.79 ± 0.78 ($n = 77$). Although mean brood size varied from year to year, the differences were not significant (Table 6). Like clutch size, brood size was as high as that recorded for any tundra nesting peregrine population (Table 7).

Nest ledges used by peregrines were accessible. Consequently, young peregrines often left the ledge on foot. Precise

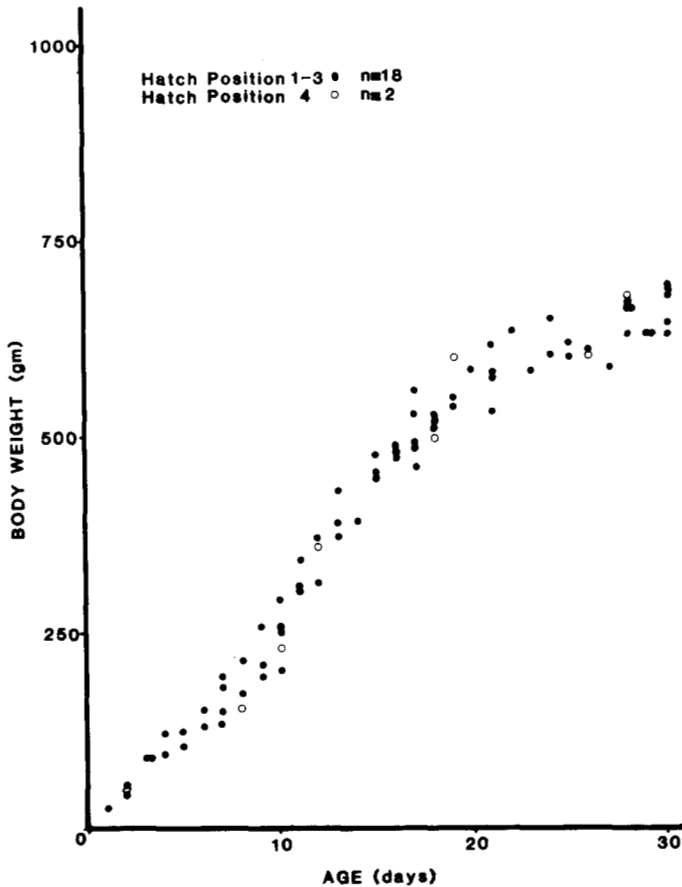


FIG. 6. Relationship between weight and age in male nestling peregrine falcons of different hatch positions in broods that hatched asynchronously.

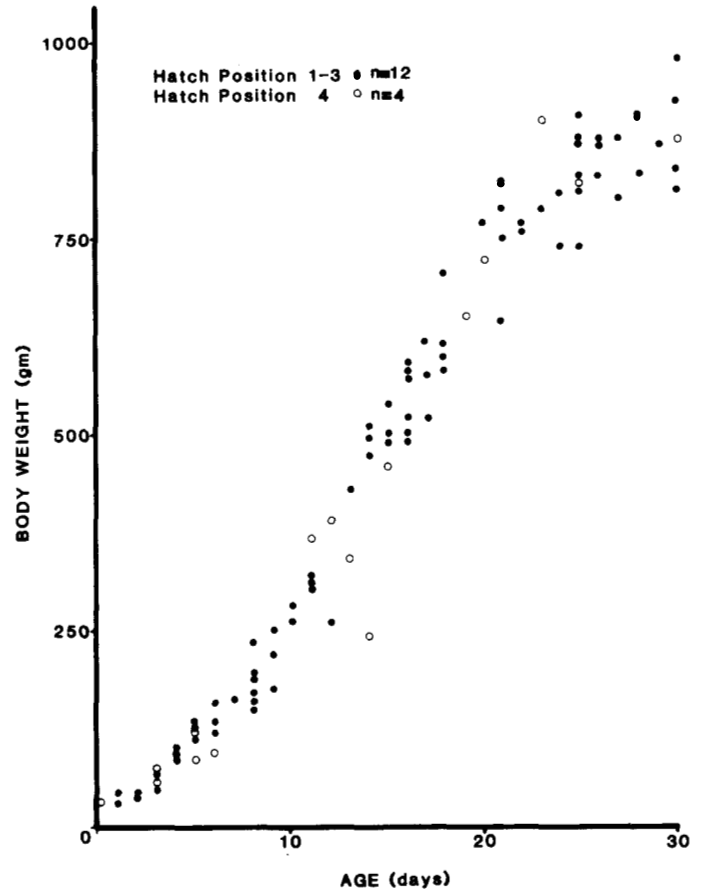


FIG. 7. Relationship between weight and age in female peregrine falcons of different hatch positions in broods that hatched asynchronously.

TABLE 6. Number of broods of different sizes for peregrine falcons nesting at Rankin Inlet, N.W.T., 1981-85

Year	Number of broods of following sizes				Total	Mean \pm S.D.
	1	2	3	4		
1981	2	6	6	1	15	2.40 \pm 0.83
1982	0	5	7	2	14	2.79 \pm 0.70
1983	0	6	6	2	14	2.71 \pm 0.73
1984	0	5	5	4	14	2.93 \pm 0.83
1985	1	2	12	5	20	3.05 \pm 0.76
All years	3	24	36	14	77	2.79 \pm 0.78 ¹

¹1-way ANOVA $F=1.68$ $df=4,72$ $P=0.16$.

fledging dates were therefore difficult to obtain, but young birds were seen in the air as early as 19 August. At one very late nest the young did not fledge until the end of the first week of September. Adult and juvenile peregrines were rarely seen at Rankin Inlet after the end of September. Over five years, 73% of pairs were successful in fledging young. Productivity ranged from 1.84 ± 1.30 to 2.40 ± 1.11 , but there was not a significant difference among years (Table 4).

Migration

Of 202 young banded on the study area between 1981 and

TABLE 7. Clutch and brood sizes for peregrine falcon populations from different studies

Reference	Region	Subspecies	Clutch size (n)	Brood size (n)
Hickey (1942)	Eastern U.S.A. (pre-DDT)	<i>F.p. anatum</i>	3.72 (282)	3.05 (124)
Ratcliffe (1980)	Great Britain	<i>F.p. peregrinus</i>	3.66 (479)	2.57 (93)
Cade (1960)	Alaska	<i>F.p. tundrius</i>	2.87 (24)	2.41 (58)
Haugh (1976)	Alaska	<i>F.p. tundrius</i>	2.67 (77)	—
Burnham and Mattox (1984)	Greenland	<i>F.p. tundrius</i>	—	2.80 (73)
Kuyt (1980)	Keewatin District, N.W.T.	<i>F.p. tundrius</i>	3.31 (13)	2.88 (16)
Calef and Heard (1979)	Northeastern Keewatin District, N.W.T.	<i>F.p. tundrius</i>	—	2.45 (13) and 2.95 (22)
This study	Rankin Inlet, Keewatin District, N.W.T.	<i>F.p. tundrius</i>	3.62 (84)	2.79 (77)

1985, 8 (4%) were recovered during migration or on the wintering grounds (Fig. 8, Table 8). Four were trapped and released by wildlife officials on barrier islands off the coasts of Virginia, North Carolina, and Texas. One bird was trapped

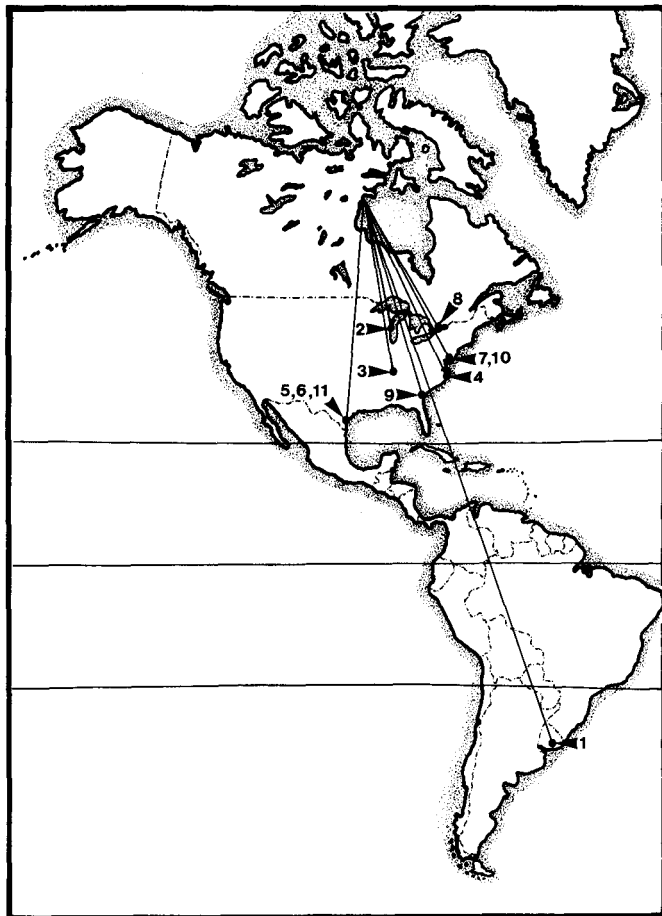


FIG. 8. Migratory pathway of peregrine falcons nesting at Rankin Inlet. See Table 8 for details of band recoveries.

inland along the shore of Lake Michigan, and another was shot on the north shore of Lake Ontario. Of 47 adult peregrines (15 male, 32 female) captured at Rankin Inlet, 3 had been captured previously on barrier islands off Georgia, Virginia, and Texas (Fig. 8, Table 8).

Only two winter recoveries were obtained for peregrines banded on the study area. Both were young of the year and both were found dead. One died of unknown causes in Kentucky in December 1983. The second was shot in Uruguay in February 1982 (Fig. 8, Table 8).

DISCUSSION

Morphology of Adults

Peregrine falcons are known to nest at latitudes as high as 77°N in North America (White, 1968) and 78°N in Eurasia (Dement'ev, 1951). Not surprisingly, there has been some degree of ecological divergence in peregrines nesting under arctic conditions, mainly in terms of morphology, the timing of life history events, and migratory habits. Peregrines from north of the coniferous forest in North America and from Greenland have been assigned to a separate subspecies, *Falco peregrinus tundrius* White (1968), distinct from the two other North American forms, *F.p. anatum* Bonaparte and *F.p. pealei* Ridgway.

Although within the tundra biome, the Rankin Inlet population occurs at a latitude of only 63°N, south of populations considered *F.p. anatum* from the Yukon River in Alaska and from the Mackenzie River Valley of the N.W.T. (Ambrose *et al.*, 1983; Bromley and Matthews, in press). However, the similarity between the timing of events in the breeding cycle of the Rankin Inlet population and that of populations in High Arctic locations (Salmonsens, 1950; Cade, 1960), coupled with the known weather patterns of the Canadian barrenlands, suggests that these birds are breeding under climatic conditions as severe as any in the enormous range of this species. Considering this, one might expect to see close similarity between adults at Rankin Inlet and those nesting at the highest latitudes. Morphometrically, however, the birds nesting at Rankin Inlet appear

TABLE 8. Band recoveries of peregrine falcons nesting at Rankin Inlet, N.W.T.

Number	Sex	Banded	Age	Recovered	Age	How recovered
1	Male	Rankin Inlet August 1981	Nestling	Cerro Chato, Uruguay February 1982	Juvenile	Shot
2	Male	Rankin Inlet July 1982	Nestling	Cedar Grove, Wisconsin October 1982	Juvenile	Trapped and released
3	Male	Rankin Inlet August 1983	Nestling	Simpson County, Kentucky December 1983	Juvenile	Found dead
4	Female	Rankin Inlet August 1983	Nestling	Corolla, North Carolina October 1983	Juvenile	Trapped and released
5	Female	Rankin Inlet July 1982	Nestling	San Padre Island, Texas October 1982	Juvenile	Trapped and released
6	Female	Rankin Inlet August 1983	Nestling	San Padre Island, Texas October 1983	Juvenile	Trapped and released
7	Female	Rankin Inlet August 1984	Nestling	Chincoteague, Virginia October 1984	Juvenile	Trapped and released
8	Female	Rankin Inlet August 1985	Nestling	Matchedash Bay, Ontario September 1985	Juvenile	Shot
9	Female	Cumberland Island, Georgia October 1976	Juvenile	Rankin Inlet May 1983	Adult	Trapped and released
10	Female	Assateague Island, Virginia September 1979	Juvenile	Rankin Inlet July 1982	Adult	Trapped and released
11	Female	San Padre Island, Texas Spring 1984	Yearling	Rankin Inlet June 1985	Adult	Trapped and released

intermediate between *anatum* birds from the boreal forest and those specimens used by White (1968) to define *F.p. tundrius*. The specimens used by White (1968) were most often from northern Alaska and islands in the Arctic Archipelago, whereas Rankin Inlet approaches the southern limit of the range reported for *F.p. tundrius*. These results suggest the existence of a cline of intergradation between the two populations.

White (1968) reported intergrading plumage characteristics between *tundrius* and *anatum* for specimens collected as far north as the south end of Southampton Island, N.W.T. (63–64°N). In referring to a bird from Hudson Bay, which had been suggested as a type specimen in an earlier subspecies proposal (Brisson, 1760), White could not assign it to either *tundrius* or *anatum*. The presence of some dark plumages in the population at Rankin Inlet is testament to such intergradation and provides additional support for the hypothesis that a latitudinal cline of variation exists for *Falco peregrinus* in North America.

Density and Nest Site Characteristics

The density of the peregrines in the study area is one of the highest recorded in North America, second only to that for a population of *F.p. pealei* on the Queen Charlotte Islands, where a mean internest distance of 1.6 km was calculated (Beebe, 1960). The mean internest distance at Rankin Inlet is lower than at any other arctic location on record. The figure of one pair for every 17 km² also illustrates the unusually high density of peregrines in the Rankin Inlet area relative to other arctic populations. Fyfe (1969), for example, estimated a density of one pair per 50 km² for "optimum" habitat on the N.W.T. mainland and the arctic islands, Burnham (1975) estimated one pair per 200 km² on his study area in western Greenland, and Falk and Møller (in press) estimated a density of one pair per 240 km² for southern Greenland.

Cade (1960) suggested that peregrine falcons select nest sites that provide protection from wind and storms. Burnham (1975) noted that exposure of nests in Greenland averaged due south, and he concluded that choice of a nest site is ultimately determined by a combination of warmth and the presence of overhanging rock. Considering the severity of arctic environments, peregrines might be expected to select preferentially those cliffs with a southern exposure and thus take advantage of any beneficial microclimatic characteristics offered by such positions.

Peregrines at Rankin Inlet rarely used nests under overhanging rock, but the majority (20/29) of nest cliffs used did have a southern component to their exposure. This, however, might indicate predominant cliff orientation rather than preference by the birds. Rock outcrops in the study area are oriented along a northwest-southeast axis; consequently, cliff faces most often faced either southwest or northeast. Cliff faces were created on southwest faces by the plucking action of glaciers that at one time advanced from the northeast. Thus many of the precipitous cliffs in the area had a southwestern exposure. Furthermore, pairs nesting on north-facing sites showed no significant difference in the number of young fledged compared to a sample that nested on cliffs with a southern exposure. It seems probable that nest site availability and territorial behaviour were the major factors determining nest site selection.

The use of stick nests of ravens (*Corvus corax*) and raptor species, particularly rough-legged hawks, is not unusual for arctic peregrines. Calef and Heard (1979) reported that 30% of

peregrine falcon nest sites at Wager Bay and on the Melville Peninsula, N.W.T., were old stick nests. In many areas nest-building species provide a platform on ledges that otherwise would be too small for peregrines to use; and these nests are often located in areas completely inaccessible to mammalian predators. Such structures also provide loose substrata for scrapes on rock ledges that would otherwise lack them. Indeed, much of the soil on cliff ledges, including heavily vegetated examples, may have its origin in ancient stick nests of species like the rough-legged hawk. Around Rankin Inlet at least, the use of the area by breeding rough-legged hawks greatly increases the number and variety of nest ledges available to peregrines.

Arrival on the Breeding Grounds

Alliston and Patterson (1978) summarized spring migration and arrival information for peregrine populations north and west of Hudson Bay. Although this information is limited, it tends to agree with our observations. The spring arrival of peregrines in the Keewatin was on average two to three weeks later than in interior Alaska (Cade, 1960; White, 1969). This difference reflects the more severe climate in northwestern Hudson Bay, even though the two areas are at similar latitudes. Observations at Rankin Inlet support the conclusion that the timing of migration of adult peregrines into the areas north and west of Hudson Bay closely parallels that of populations in Greenland (Salmonsens, 1950) and the Eurasian tundra (Dement'ev, 1951).

The interval between spring arrival and clutch initiation in arctic nesting populations of the peregrine is very brief relative to populations at southern latitudes. Such a small interval has given rise to speculation that courtship may be completely eclipsed in northern populations or that courtship may be initiated on the wintering grounds or on migration (Cade, 1960). The asynchronous arrival of marked pairs observed at Rankin Inlet provides evidence against the latter speculation.

Prey Use

Peregrine falcons prey on a wide range of avian species. Even in areas where the avifauna is impoverished, peregrines may prey on a large percentage of all species represented (Cade, 1960; Burnham, 1975). Cade (1960) found that arctic peregrines also take a wide variety of prey species, concluding that no one species constituted a major portion of the diet. At Rankin Inlet, relative frequency of prey use indicated that although a wide range of species was taken, the most important prey species were the four locally breeding passerines and ptarmigan during their spring migration. The heavy use of passerines by tundra nesting peregrines has also been noted in Greenland (Burnham, 1975; Harris and Clement, 1975; Burnham and Mattox, 1984; Falk *et al.*, 1986). Young passerines were often just out of the nest as young peregrines were hatching; similar synchrony has been documented in Greenland (Harris and Clement, 1975; Falk *et al.*, 1986). These fledglings, with their poorly developed powers of flight, were easily caught by adult peregrines, explaining the predominance of their remains at all nest sites at Rankin Inlet. Harris and Clement (1975) believed that adult passerines are also more vulnerable at this time as they begin the moult.

Peregrines at Rankin Inlet arrive on the breeding grounds before the majority of their prey species. Thus snow buntings and ptarmigan were important for the entire population at this time of year. The use of these birds contrasts with other studies

stressing the spring arrival of northern peregrines being closely synchronized with the arrival of waterfowl (Dement'ev, 1951; Cade, 1960; White, 1969). With the possible exception of geese, waterfowl arrive on the study area some weeks after peregrines, a point that again highlights the severity of the climate on the study area relative to most other studies of the peregrine in the North.

Arctic ground squirrels and black guillemots were found in colonies throughout the study area. Their pattern of dispersion at all times of the year was clumped. For this reason only peregrine pairs nesting in close proximity to these colonies used these species to any extent. Pairs specializing on these species would enjoy an advantage in terms of the amount of biomass delivered per prey item. However, these pairs always supplemented the diet with fledgling passerines, a point that demonstrates the widespread availability of these small birds as a prey source.

The use of ground squirrels by the peregrines at Rankin Inlet and the use of lemmings during the peak year of 1985 highlight the considerable plasticity of the peregrine falcon in terms of diet. The peregrine is considered a bird predator (Hickey and Anderson, 1969; Cade, 1982) and is thought not to show any numerical response to increased microtine abundance at arctic latitudes (Cade, 1960). At Rankin Inlet peregrines did use lemmings during the microtine peak of 1985 and showed a numerical increase commensurate with that of local rough-legged hawks, a species known to track microtine abundance (Hagen, 1969). This response and its implications regarding variations in population size and breeding success have been documented extensively elsewhere (Court, 1986; Court *et al.*, in press). It should be noted here, though, that the most parsimonious explanation of the dramatic changes in reproductive success and population size of peregrines breeding at Rankin Inlet in 1985 was the existence of a peak in microtine abundance.

The Breeding Season

Cade (1960:182) summarized nesting records for northern peregrines and concluded that "in arctic latitudes peregrines must lay their eggs not later than the beginning of the third week of June to ensure successful rearing of young, because by mid-September the bulk of their food is gone." Generally this is true for the Rankin Inlet population, as most clutches were completed by 15 June, giving dates of independence, based on Sherrod (1983), as early as the third week in September. However, there existed some cases where young may have fledged as late as the end of the first week in September, giving a date of independence well into October. At Rankin Inlet young peregrines were rarely seen after the end of September, suggesting that many begin migration very shortly after, or perhaps even before, they have gained independence. It is possible that young, not fully independent of their parents when migration begins, are fed as they move south or steal or scavenge the kills of parents, siblings, other peregrines, or perhaps other raptors during this period. Examples of such behaviour have been reported for migrating peregrines (Dekker, 1980).

Overall, the length of the breeding season for peregrines in the study area was not substantially different from that of other populations at high latitudes. There is nothing to suggest any difference in the length of most parameters of breeding chronology in this population and those previously reported for the species. The only periods that were noticeably shortened were

the pre-laying courtship period and perhaps the total time of post-fledging dependence. The total time with eggs was also shorter than in southern populations, as incubation was initiated before clutch completion. This behaviour, and the resulting hatch asynchrony, is commonly reported in the Arctic (Enderson *et al.*, 1972; Burnham and Mattox, 1984; R. Fyfe, pers. comm. 1983) but is rare at more temperate latitudes (Ratcliffe, 1980).

Calef and Heard (1979) summarized data on brood size and productivity for peregrine falcons nesting in the northeastern Keewatin District and Melville Peninsula and concluded that these populations were the most productive of the *tundrius* subspecies. From Table 7, it is clear that, except for populations in Alaska, most other populations of *F.p. tundrius* are equally productive. It is also apparent that the arctic birds are as productive as some of the most productive populations from temperate latitudes. This was illustrated by the lack of a significant difference in clutch size between the Rankin Inlet population and the pre-pesticide sample of Hickey (1942). This comparison is important because some authors (Hickey, 1942; Cade, 1960) have suggested that northern peregrines lay smaller clutches, and consequently fledge fewer young, than populations at more southerly latitudes. This suggestion opposes trends seen in a great many other species and is contrary to general hypotheses that directly relate latitude and clutch size (Ashmole, 1961; Ricklefs, 1980).

Over five years, 73% of pairs to obtain territories were successful in fledging young. This figure is lower than the maximum success rate of 85% previously reported for Keewatin peregrines (Calef and Heard, 1979) and highlights the difficulty of comparing productivity data from intensive studies, such as that at Rankin Inlet, to data solely from surveys conducted during the nestling phase of the breeding cycle. Surveys performed during late incubation or nestling periods, especially those using aircraft, are likely to overlook some pairs that did not lay or failed during early incubation. As a result, measures of reproductive success based on number of pairs on territories tend to be exaggerated and are of limited value for comparison here. Studies of a gyrfalcon (*Falco rusticolis*) population conducted over the entire breeding season showed that only 59% of all pairs on territory produce young (Poole, 1987). Peregrines from Rankin Inlet were, on average, more successful at every stage of the breeding cycle compared to the gyrfalcons studied by Poole (1987).

The number of young fledged per occupied territory ranged from 1.84 ± 1.30 to 2.40 ± 1.11 , averaging about 2.0 young fledged per occupied territory per year. In other arctic populations this measure ranges to as high as 2.21 (Calef and Heard, 1979) and 2.6 (Burnham and Mattox, 1984) young fledged per occupied territory. Nevertheless, as mentioned above, comparisons of the number of young fledged per occupied territory from different studies may be of limited value, except for those populations in which the number of pairs present is measured early in the nesting season. This fledging success for birds in the Rankin Inlet population suggests that in most years these falcons had little difficulty raising most young to fledging age. Such production reflects an abundant prey base and few decimating factors, such as parasites or predators. *Protocalliphora* (Hickey, 1942; Poole, 1987) and argasid tick infestations (Oliphant *et al.*, 1976) have been implicated occasionally in nestling mortality of falcons. No evidence of these parasites was obtained over the five years of the study. Potential nest predators, such as the arctic fox (*Alopex lagopus*), were rarely seen on the study area

during the five field seasons, and snowy owls (*Nyctea scandiaca*) were seen regularly only in 1985. The fact that individual falcons in this population did not hesitate to strike snowy owl decoys and occasionally struck humans as they approached the nest suggests that the importance of other raptors and mammals as potential nest predators cannot be overlooked.

Overall, our findings, combined with those of Alliston and Patterson (1978), Calef and Heard (1979), and Kuyt (1980), demonstrate that the Keewatin District of the N.W.T. has some of the densest and most productive nesting populations of *Falco peregrinus* to be found anywhere in the world. Particularly striking is the fact that huge areas of this district have yet to be surveyed for raptors. It is also gratifying to note that the productivity of this population appears to be sustained despite continuing pollution of the wintering range with organochlorine biocides (Peakall, 1976). Nevertheless, it should be noted that a certain proportion of nesting failures at Rankin Inlet each year were attributable directly to pesticide pollution (Court *et al.*, unpubl. data).

Migration

Earlier authors speculated that the large number of peregrines migrating along the eastern seaboard of the United States included many that were of arctic origin (Cade, 1960; White, 1968). Subsequent banding studies established that many of these birds originate from breeding populations considered either *F.p. anatum* or *F.p. tundrius* and from as far apart as the Yukon River in Alaska (Henny *et al.*, 1982), the northeastern Keewatin District of the N.W.T. (Calef and Heard, 1979), and Greenland (Burnham and Mattox, 1984; Falk and Møller, in press). Our data show that peregrines nesting along the west coast of Hudson Bay also use a similar pathway. Band recoveries from the Great Lakes, however, show that migration is not restricted exclusively to the eastern seaboard.

White (1968) concluded that *F.p. tundrius* would winter as far north as the Florida Keys and Baja California to as far south as Chile and Argentina. The recovery of a juvenile peregrine from Rankin Inlet in Kentucky did not match the reported winter range. However, a second bird from the Rankin Inlet population was recovered in Uruguay. The wintering range described by White (1968) should not be considered as strictly unique to *tundrius*, however, as *anatum* peregrines from boreal regions of Canada have been recovered from as far south as Columbia and Chile (U. Banasch, Canadian Wildlife Service, pers. comm. 1987). Thus, it is likely that northern populations of *anatum* and *tundrius* occur over similar ranges during winter.

ACKNOWLEDGEMENTS

Logistical assistance and funding for field work was provided by the Department of Renewable Resources, Government of the Northwest Territories, the World Wildlife Fund—Canada, the Canadian Wildlife Service—Environment Canada, the Science Advisory Board of the N.W.T. (Summer Student Employment, 1982-84), the Boreal Institute for Northern Studies (Northern Science Training Grant 55-51799), the Natural Sciences and Engineering Research Council (NSERC) (Operating Grant to D.A. Boag [A2010] and Postgraduate Scholarship [3894250] to G.S. Court), and the Max and Marjorie Ward Scholarship. The authors gratefully acknowledge the assistance of all employees of the Department of Renewable Resources at Rankin Inlet, particularly the field assistance of M. Bradley, P. Kolit, R. Mulders, M. Sawatsky, and F. Ayaruak. M. Bradley kindly provided data on nest site occupancy and egg production for 1985. G. Erickson and H.

Armbruster assisted with the trapping of adult falcons in 1983 and 1985. P. Trefrey, H. Trefrey, and H. Armbruster, of the Canadian Wildlife Service Endangered Species Facility at Wainwright, allowed us to obtain morphometric data from adult peregrines in their care. K. Poole and U. Banasch reviewed the manuscript. We are grateful to C. Shank and an anonymous reviewer for constructive criticism of an earlier draft of this paper.

REFERENCES

- ALLISTON, W.G., and PATTERSON, L.A. 1978. A preliminary study of peregrine falcon populations in the Polar Gas Area, districts of Franklin and Keewatin, N.W.T. LGL Environmental Research Associates, Toronto. 112 p. Available at The Boreal Institute for Northern Studies Library, Biological Sciences Building, University of Alberta, Edmonton, Alberta, Canada T6G 2E9.
- AMBROSE, R., SCHEMPF, P., and HUNTER, R. 1983. American peregrine falcon (*Falco peregrinus anatum*) studies on the Upper Yukon River, Alaska, 1983. Unpubl. report. U.S. Fish and Wildlife Service, Juneau, Alaska. 19 p. Available at United States Fish and Wildlife Service, 1412 Airport Way, Fairbanks, Alaska 99701, U.S.A.
- ASHMOLE, N.P. 1961. The biology of certain terns. Unpubl. Ph.D. thesis, Oxford University, Oxford.
- BEEBE, F.L. 1960. The marine peregrines of the northwest pacific coast. *Condor* 62:145-189.
- BRISSON, M.J. 1760. Ornithologie, en Méthod contenant la division des oiseaux. Cited in: White, C.M. 1968. Diagnosis and Relationships of the North American tundra-inhabiting peregrine falcons. *Auk* 85:179-191.
- BROMLEY, R.G. In press. Status of peregrine falcons in the Kitikmeot, Baffin, and Keewatin Regions of the Northwest Territories, 1982 to 1985. In: Cade, T.J., Enderson, J.H., Thelander, C.G., and White, C.M., eds. *Peregrine Falcon Populations: Their Management and Recovery*. Proceedings of the 1985 International Peregrine Conference, Sacramento.
- _____. and MATTHEWS, S. In press. Status of the peregrine falcon (*Falco peregrinus anatum*) in the Mackenzie River Valley, Northwest Territories, 1969 to 1985. In: Cade, T.J., Enderson, J.H., Thelander, C.G., and White, C.M., eds. *Peregrine Falcon Populations: Their Management and Recovery*. Proceedings of the 1985 International Peregrine Conference, Sacramento.
- BURNHAM, W.A. 1975. Breeding biology and ecology of the peregrine falcon in Greenland. Unpubl. M.Sc. thesis, Brigham Young University, Provo, Utah. 57 p.
- _____. and MATTOX, W.G. 1984. Biology of the peregrine and gyrfalcon in Greenland. *Meddelelser om Grønland Bioscience* 14. 28 p.
- CADE, T.J. 1960. Ecology of the peregrine and gyrfalcon populations in Alaska. University of California Publications in Zoology 63:151-290.
- _____. 1982. *The Falcons of the World*. London: William Collins Sons. 192 p.
- _____. and FYFE, R.W. 1970. The North American peregrine survey, 1970. *Canadian Field-Naturalist* 84:231-245.
- CALEF, G.W., and HEARD, D.C. 1979. Reproductive success of peregrine falcons at Wager Bay and on Melville Peninsula, Northwest Territories. *Auk* 96:662-674.
- CONOVER, W.J. 1980. *Practical Nonparametric Statistics*. New York: John Wiley and Sons. 492 p.
- COURT, G.S. 1986. Some aspects of the reproductive biology of tundra peregrine falcons. Unpubl. M.Sc. thesis, University of Alberta, Edmonton, Alberta. 121 p.
- _____. BRADLEY, D.M., GATES, C.C., and BOAG, D.A. In press. The population biology of peregrine falcons in the Keewatin District of the Northwest Territories, Canada. In: Cade, T.J., Enderson, J.H., Thelander, C.G., and White, C.M., eds. *Peregrine Falcon Populations: Their Management and Recovery*. Proceedings of the 1985 International Peregrine Conference, Sacramento.
- DEKKER, D. 1980. Hunting success rates, foraging habits, and prey selection of peregrine falcons migrating through Alberta. *Canadian Field-Naturalist* 94:371-382.
- DEMENT'EV, G.P. 1951. Translated 1966. Order Falconiformes (Accipitres). In: Dement'ev, G.P., and Gladkov, N.A., eds. *Birds of the Soviet Union*. Vol. I. Jerusalem: S. Monson. 71-378.
- ENDERSON, J.H., TEMPLE, S.A., and SWARTZ, L.G. 1972. Time-lapse photographic records of nesting peregrine falcons. *Living Bird* 11:113-128.
- FALK, K., and MØLLER, S. In press. Status of the peregrine falcon (*Falco peregrinus*) in South Greenland: population density and reproduction. In: Cade, T.J., Enderson, J.H., Thelander, C.G., and White, C.M., eds.

- Peregrine Falcon Populations: Their Management and Recovery. Proceedings of the 1985 International Peregrine Conference, Sacramento.
- _____ and BURNHAM, W.A. 1986. The peregrine falcon (*Falco peregrinus*) in South Greenland: nesting requirements, phenology, and prey selection. Dansk Ornithologisk Forenings Tidsskrift 80:113-120.
- FYFE, R.W. 1969. The peregrine falcon in northern Canada. In: Hickey, J.J., ed. Peregrine Falcon Populations: Their Biology and Decline. Madison: University of Wisconsin Press. 101-114.
- _____, TEMPLE, S.A., and CADE, T.J. 1976. The 1975 North American peregrine falcon survey. Canadian Field-Naturalist 90:228-273.
- GODFREY, W.E. 1986. The Birds of Canada. Ottawa: National Museums of Canada. 595 p.
- HAGEN, Y. 1969. Norwegian studies on the reproduction of birds of prey and owls in relation to micro-rodent fluctuations. Fauna 22:73-126.
- HARRIS, J.T., and CLEMENT, D.M. 1975. Greenland peregrines at their eyries: a behavioral study of the peregrine falcon. Meddelelser om Grønland 205:1-28.
- HAUGH, J.R. 1976. Population changes in Alaskan arctic peregrines. Canadian Field-Naturalist 90:359-361.
- HENNY, C.J., WARD, P., RIDDLE, K., and PROUTY, R. 1982. Migratory peregrine falcons, *Falco peregrinus*, accumulate pesticides in Latin America during winter. Canadian Field-Naturalist 96:333-338.
- HICKEY, J.J. 1942. Eastern population of the duck hawk. Auk 59:176-204.
- _____ and ANDERSON, D.W. 1969. The peregrine falcon: life history and population literature. In: Hickey, J.J., ed. Peregrine Falcon Populations: Their Biology and Decline. Madison: University of Wisconsin Press. 3-42.
- KUYT, E. 1980. Distribution and breeding biology of raptors in the Thelon River area, Northwest Territories, 1957-1969. Canadian Field-Naturalist 94:121-130.
- MAHER, W.J. 1980. Growth of the horned lark at Rankin Inlet, Northwest Territories. Canadian Field-Naturalist 94:405-410.
- MINISTRY OF TRANSPORT. Unpubl. records available at Environment Canada, Atmospheric Environment Service, Twin Atria Building, 4999 - 98 Avenue, Edmonton, Alberta, Canada T6B 2X3.
- NETHERSOLE-THOMPSON, D. 1931. Observations on the peregrine falcon. In: Ratcliffe, D.A. 1980. The Peregrine Falcon. Calton: T. and A.D. Poyser. 416 p.
- OLIPHANT, L.W., THOMPSON, W.J.P., DONALD, T., and RAFUSE, R. 1976. Present status of the prairie falcon in Saskatchewan. Canadian Field-Naturalist 90:365-368.
- PEAKALL, D.B. 1976. The peregrine falcon (*Falco peregrinus*) and pesticides. Canadian Field-Naturalist 90:301-307.
- POOLE, K.G. 1987. Aspects of the ecology, food habits and foraging characteristics of gyrfalcons in the central Canadian Arctic. Unpubl. M.Sc. thesis, University of Alberta, Edmonton, Alberta. 120 p.
- POSTUPULSKY, S. 1974. Raptor reproductive success: some problems with methods, criteria, and terminology. In: Hamerstrom, F.E., Harrell, B.E., and Olendorff, R.R., eds. Management of Raptors. Vermillion, South Dakota: Raptor Research Foundation, Raptor Research Report No. 2. 21-31.
- RATCLIFFE, D.A. 1980. The Peregrine Falcon. Calton: T. and A.D. Poyser. 416 p.
- RICKLEFS, R.E. 1980. Geographical variation in clutch size among passerine birds: Ashmole's hypothesis. Auk 97:38-49.
- SALMONSEN, F. 1950. The Birds of Greenland, Vol. I. Copenhagen: Munksgaard. 607 p.
- SHERROD, S.K. 1983. Behavior of fledgling peregrines. Ithaca: The Peregrine Fund. 202 p.
- WHITE, C.M. 1968. Diagnosis and relationships of the North American tundra-inhabiting peregrine falcons. Auk 85:179-191.
- _____. 1969. Breeding Alaskan and arctic migrant populations of the peregrine. In: Hickey, J.J., ed. Peregrine Falcon Populations: Their Biology and Decline. Madison: University of Wisconsin Press. 45-52.
- WRIGHT, G.M. 1967. Geology of the south-eastern barren-grounds, parts of the Districts of Mackenzie and Keewatin. Ottawa: Queen's Printers. 91 p.